

Aplodontia rufa. By Leslie N. Carraway and B. J. Verts

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Aplodontia Richardson, 1829b

Aplodontia Richardson, 1829b:334. Type species *Aplodontia leporina* Richardson (= *Anisonyx rufa* Rafinesque).

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuroomorpha, Superfamily Aplodontoidea, Family Aplodontidae, Genus *Aplodontia* (Hall, 1981; Miller and Kellogg, 1955; Simpson, 1945). One living species is recognized (Hall, 1981).

Aplodontia rufa (Rafinesque)

Mountain beaver

Anisonyx? *rufa* Rafinesque, 1817:45. Type locality "Neighbourhood of the Columbia River."

Aplodontia leporina Richardson, 1829b:435. No locality, but near Columbia River implied. Based on a specimen (no. 17) in the "Hudson's Bay Museum."

Aplodontia rufa: Merriam, 1886:316. First formal use of current name combination.

Aplodontia major Merriam, 1886:316. Type locality "Placer county, Cal."

Aplodontia major Merriam, 1899:20. Type locality "Queniult [sic] Lake, Olympic Mts., [Grays Harbor Co.], Washington."

Aplodontia olympica Merriam, 1899:20. Type locality "Queniult [sic] Lake, Olympic Mts., [Grays Harbour Co.], Washington."

Aplodontia pacifica Merriam, 1899:19. Type locality "Newport, mouth of Yaquina Bay, [Lincoln Co.], Oregon."

Aplodontia phaea Merriam, 1899:20. Type locality "Pt. Reyes, Marin Co., California."

Aplodontia chryseola Kellogg, 1914:295. Type locality "Jackson Lake, Siskiyou County, California, altitude 5900 feet."

Aplodontia nigra Taylor, 1914:297. Type locality "Point Arena, Mendocino County, California."

Aplodontia humboldtiana Taylor, 1916a:21. Type locality "Carroll, Humboldt County, California."

CONTEXT AND CONTENT. Context same as for genus. Seven subspecies are recognized currently (Dalquest and Scheffer, 1945; Hall, 1981):

A. r. californica (Peters, 1864:179). Type locality "near main top." Type locality restricted to crest of Sierra Nevada Mountains, California, by Hall (1941). (*major* Merriam, 1886, a synonym).

A. r. humboldtiana Taylor, 1916a:21, see above.

A. r. nigra Taylor, 1914:297, see above.

A. r. pacifica Merriam, 1899:19, see above.

A. r. phaea Merriam, 1899:20, see above.

A. r. rainieri Merriam, 1899:21. Type locality "Paradise Creek, south side Mt. Rainier, [Pierce Co.], Washington (alt., 5200 ft.)." (*columbiana* Taylor, 1916b, a synonym).

A. r. rufa (Rafinesque, 1817:45), see above. (*leporina* Richardson, 1829b, *olympica* Merriam, 1899, *chryseola* Kellogg, 1914, and *grisea* Taylor, 1916b, are synonyms).

DIAGNOSIS. The mountain beaver (Fig. 1) has the general appearance of a medium-sized muskrat (*Ondatra zibethicus*) except the tail is well furred and exceedingly short. Other characteristics of the species include a pelage uniformly dark brown except for a white spot below each ear; skull (Fig. 2) flattened dorsoventrally and broadened posteriorly; cheekteeth lacking complex folds of enamel and each appears as a single puddle of dentine surrounded by enamel; and maxillary cheekteeth with a labial spinelike projection of enamel, whereas the mandibular cheekteeth have a similar lingual projection. The auditory bulla is flask-shaped, a postorbital process is lacking,

the palate is broad and extends beyond the toothrows, and the coronoid process is high and curved posteriorly (McLaughlin, 1984). The origin of the masseter muscle is limited to the ventral surface of the zygoma (Kurtén and Anderson, 1980). The baculum (Fig. 3) is thin, convex dorsally, concave ventrally, and forked distally; each distal terminus is equipped with a condylelike process, whereas the proximal terminus is notched (Burt, 1960). The bifurcation was interpreted to indicate fusion of separate elements, thus a homology between epipubic bones in marsupials and the baculum in other mammals was inferred (Jellison, 1945b). The os clitoridis (Fig. 3) is about 2 by 6 mm, curved, and forked proximally (Scheffer, 1942).

GENERAL CHARACTERS. The incisors are strong, flattened anteriorly, and without grooves; the enamel is yellowish orange. Cheekteeth are hypsodont (Rensberger, 1978) and ever-growing, and are arranged in straight, parallel rows in the maxilla, but slightly concave rows in the mandible. P4 is characterized by the loss of a barrier between the transverse-median and posterointernal basins and loss of the anterointernal cingular ridge that brings the protoconule to the margin of the tooth (McGrew, 1941). Lower molars exhibit little reduction of the protoconid (McGrew, 1941). The barrier between the two talonid lakes on p4 has disappeared causing the talonid to occupy a single large basin. The palate extends beyond the toothrows. The dental formula is i 2/2, c 0/0, p 2/1, m 3/3, total 22. P3 is minute.

The head is flat and wide; the nose "is a little arched" (Richardson, 1829a:210). The body is thick, heavy, and covered with coarse, dull fur. The under fur is thick and covered with sparse guard hairs; the color is dark reddish or grayish brown. The venter is lighter than the dorsum (Maser et al., 1981). The limbs are short and robust, and equipped with strong, five-toed feet; the sole is naked to the heel. The feet are plantigrade (Hubbard, 1922). The toes, except for the partially opposable pollex, have long, strong, curved, sharp, and laterally compressed claws (Lewis, 1949); the claw on the pollex is short and blunt, and has been referred to as a nail (Hill, 1937). The claws are cream or light tan. The tail is scarcely visible as it barely extends beyond the fur.

Mean (\pm SE) monthly mass of juveniles ranged from 357.4 \pm 19.7 g (range, 280–440 g; n = 9) in June to a peak of 584.3 \pm 16.2 g (range, 557–645 g) in October for males and from 473.1 \pm 35.6 g (range, 330–590 g; n = 8) in June to a peak of 630 \pm 10.0 g (range, 624–640 g; n = 2) the following February for females (Lovejoy and Black, 1974). Males lost mass over winter, whereas females continued to gain. Mean (\pm SE) mass of 15 yearlings (both sexes combined) weighed 53 times between April and December was



FIG. 1. Photograph of an adult *Aplodontia rufa*. Photograph courtesy of the Weyerhaeuser Archives.

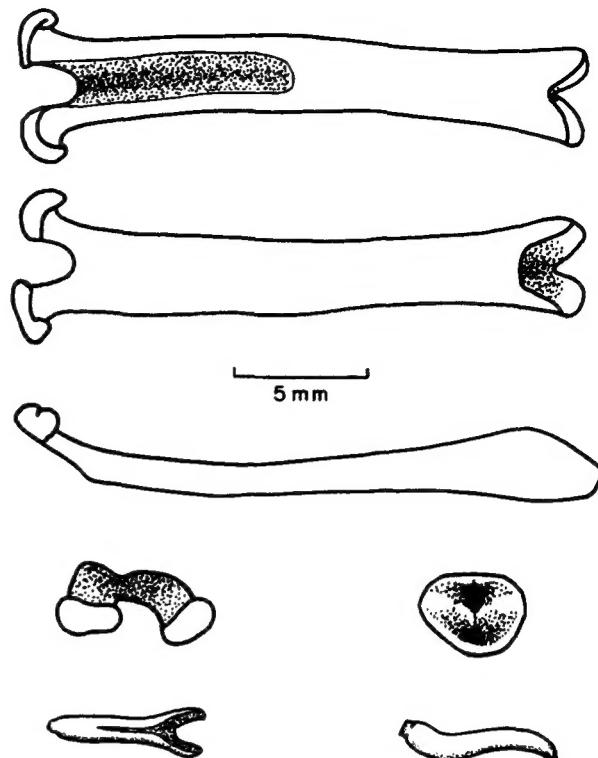


FIG. 3. Camera lucida tracings of dorsal, ventral, lateral, distal, and proximal views (top five) of the baculum of *Aplodontia rufa* of OSUFW 8742 from 2 mi. S, 1 mi. E Eddyville, Lincoln Co., Oregon, and dorsal and lateral views (bottom two) of the os clitoridis of an individual from near Redmond, King Co., Washington. Os clitoridis redrawn from Scheffer (1942:443, fig. 1). Distal is at left for all dorsal, ventral, and lateral views.

709.9 ± 9.8 g (range, 580–910 g—Lovejoy and Black, 1974). Mean mass of adults fluctuated seasonally with the peak for both sexes in July and the annual low point in March for females and April for males (Lovejoy and Black, 1974:368, fig. 1). The mean of 455 weighings for 109 adults of both sexes weighed throughout the year was 806 g; maximum mass for mountain beavers in Benton Co., Oregon, was 1,070 g for adult females and 1,130 for adult males (Lovejoy and Black, 1974). A maximum mass of 1,419 g also was reported (Maser et al., 1981). The brain mass of mountain beavers calculated from cranial volume was 7.63 g (Mace et al., 1981).

Ranges of standard measurements (in mm) were (Ingles, 1965): total length, 300–470; tail length, 20–40; length of hind foot, 55–63; ear length (13–21). Measurements for the same dimensions provided by Bailey (1936), Banfield (1974), Cowan and Guiguet (1965), Dalquest (1948), Hall (1981), Jameson and Peeters (1988), and Palmer (1954) did not exceed these values by >2 mm, except ear lengths ≤ 25 mm were reported by Dalquest (1948). However, Maser et al. (1981) listed measurements (in the same order) for mountain beavers in coastal Oregon as 238–370, 19–55, 48–63, and 21–30.

Ranges of selected cranial dimensions (in mm) for small samples from throughout the range (Finley, 1941; Kellogg, 1916; Taylor, 1918) were: basilar length, 51.1–65.4; length of nasals, 20.3–30.9; width of nasals, 8.7–14.1; length of incisive foramen, 4.5–8.7; zygomatic breadth, 46.0–64.0; mastoid breadth, 41.9–61.2; length of upper toothrow, 16.9–21.0; distance between infraorbital foramina, 14.1–18.9; and greatest length of mandible, 41.7–54.9. Most

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FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral and dorsal views of the mandible of an adult female *Aplodontia rufa* (OSUFW [Oregon State University Department of Fisheries and Wildlife mammal collection] 8743; from 2 mi. S, 1 mi. E Eddyville, Lincoln Co., Oregon). Occipitonasal length is 66.7 mm.

of the dimensions for *A. r. phaea* and *A. r. pacifica* were near the low end of the range, whereas those for *A. r. rainieri* and *A. r. californica* were near the upper end.

DISTRIBUTION. The distribution of *A. rufa* (Fig. 4) is in four disjunct groups of populations. The largest, encompassing ranges of four nominal geographic races, extends from near Merritt, British Columbia, south along the Cascade, Olympic, Coast, and Siskiyou ranges to Rio Dell, California; another extends from Mt. Shasta, California, southeastward through the Sierra Nevada Range of eastern California and extreme western Nevada; and the others exist as tiny coastal populations in California, one at Point Arena, Mendocino Co., the other near Point Reyes, Marin Co. (Dalquest and Scheffer, 1945; Hall, 1981).

FOSSIL RECORD. The family Aplodontidae is descended from the Prosciurinae, an early to middle Oligocene radiation; followed by the Allomyinae, an Oligocene-Miocene radiation; and that followed by the Aplodontinae, a later Miocene radiation (Kurtén and Anderson, 1980; Rensberger, 1975). The aplodontoid rodents are represented by the extinct Mylagaulidae and the mostly extinct Aplodontidae; only the monotypic genus *Aplodontia* is extant within Aplodontidae. The Mylagaulidae represents an early to middle Miocene radiation from the early Miocene aplodontids and exhibits extreme divergence and greater specialization. The most notable characteristic of the evolution of the Aplodontoidea is the marked progression to greater hypsodonty (McGrew, 1941; Rensberger, 1982).

As indicated by the fossil record since the late Oligocene, the geographic distributions of *Aplodontia* and its ancestors changed little. There were a few unsuccessful expansions of the range into Mongolia in the middle Oligocene (Wang, 1987), Nevada and Montana during the Oligocene (Donohoe, 1956; Rensberger, 1981; Shotwell, 1958), northcentral Oregon in the late Oligocene-early Miocene (Rensberger, 1983), and southeastern Oregon in the mid-Miocene (Shotwell, 1958). However, the mylagaulids expanded their geographic distributions into the Great Plains during the late Miocene and early Pliocene (McGrew, 1941; Shotwell, 1958). *Aplodontia* was reported from three late Pleistocene faunas in northern California, Potter Creek, Samwel Cave, and Hawver Cave, all within its present distribution (Kurtén and Anderson, 1980).

FORM AND FUNCTION. The kidneys of mountain beavers are nonlobated, the simple pelvis lacks processes in the lateral wall and contains the area cribrosa, a papilla covered with transitional type stratified epithelium, and have no Ludwig's arterioles, arteriolae verae, renal papillae, looped vasa recta, or inner zone of the medullary substance (House et al., 1963; Nungesser et al., 1960; Nungesser and Pfeiffer, 1965; Pfeiffer, 1968; Pfeiffer et al., 1960). Pfeiffer et al. (1960) reported that the kidneys have a cortical mass : medullary substance ratio of 1:1; however, Nungesser and Pfeiffer (1965) reported a cortical mass : medullary substance ratio of 1:2.9. The glomeruli near the surface of the cortex have a mean ($\pm SE$) diameter of 92 μm (range, 69–115 μm) and are concentrated at 16–27 glomeruli/mm². The glomeruli in the juxtamedullary region have a mean diameter of 140 μm (range, 112–203 μm) and are concentrated at 9–17 glomeruli/mm². The cortical nephrons are most abundant in the outer cortex, have short loops of Henle that do not enter the medulla, lack thin segments, and constitute 62–70% of the kidney nephrons (Pfeiffer et al., 1960). The medullary nephrons have only a few thin segments, none of which are associated with hair-pin turns. Unusual characteristics of the kidneys are that the loop of Henle has hair-pin turns only in the thick ascending portion, no loops connect the arteriolae rectae and venucae rectae, and the collecting duct arcades originate deep in the cortex (Pfeiffer et al., 1960). The anatomy of the kidneys support laboratory findings that mountain beavers cannot produce hypertonic urine.

Aplodontia consumed ($\pm SE$) 327 \pm 24 ml/kg (>1,000 observations) of water each 24 h; urine output at the same time was 267 \pm 25.7 ml/kg (>2,000 observations—Nungesser and Pfeiffer, 1965). The amount of water consumed was inversely related to the amount of succulent food in the diet. *A. rufa* produces urine at a rate of one-fourth to one-third of the body mass daily (Nungesser et al., 1960). Mean ($\pm SE$) urine flow was 9.05 \pm 0.68 ml/h during the day and 6.7 \pm 0.9 ml/h at night; mean urine concentration was 220 \pm 14 mOsm/l and 314.5 \pm 34 mOsm/l, respectively. The "reduced urine flow and increase in osmolarity at night . . . must be due to increased tubular reabsorption of water" (Dicker and

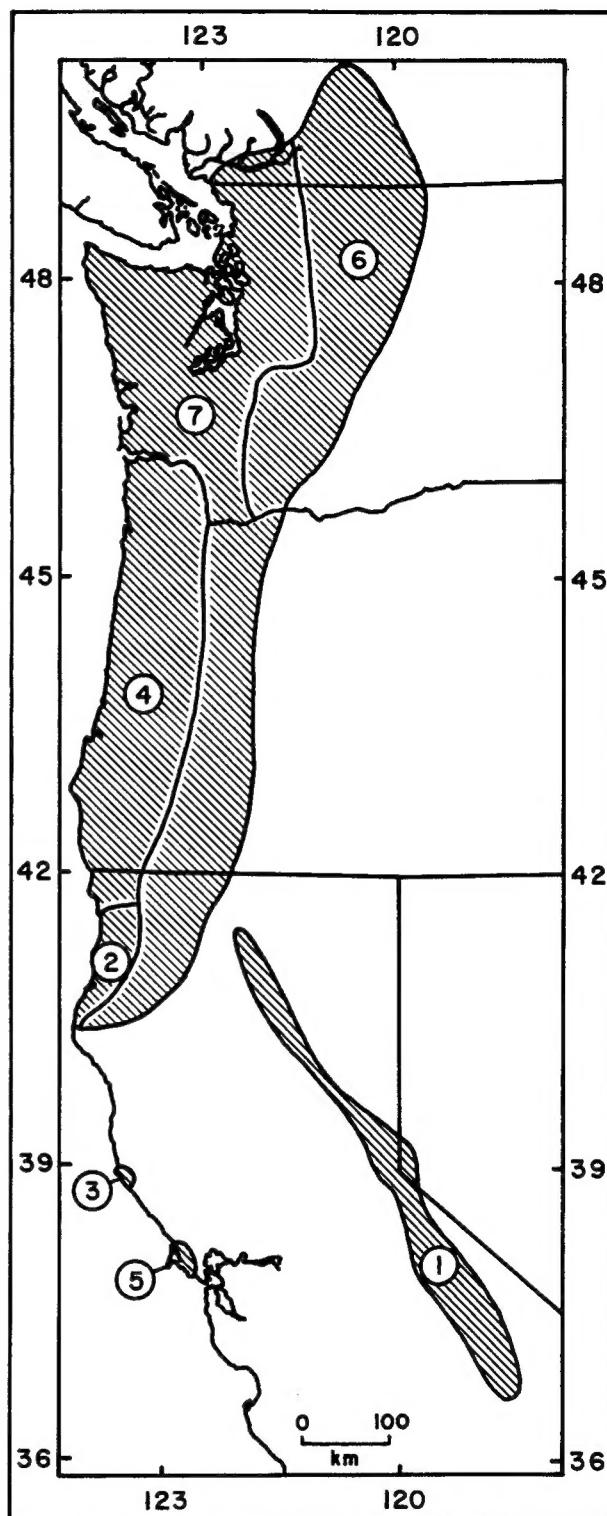


FIG. 4. Geographic distribution of *Aplodontia rufa*. Subspecies are: 1, *A. r. californica*; 2, *A. r. humboldtiana*; 3, *A. r. nigra*; 4, *A. r. pacifica*; 5, *A. r. phaea*; 6, *A. r. rainieri*; 7, *A. r. rufa* (redrawn after Dalquest and Scheffer, 1945; Hall, 1981).

Eggleton, 1964:187). Mean creatinine excretion was 1.73 \pm 0.07 mg/h during the day and 1.74 \pm 0.16 mg/h at night (Dicker and Eggleton, 1964). Hematocrits range from 28–42 and the plasma-chloride concentration is 95–103 milliequivalents/l (Nungesser and Pfeiffer, 1965). The range of the urine : plasma ratio is 1:2.0–2.46 (Nungesser et al., 1960; Nungesser and Pfeiffer, 1965; Pfeiffer et al., 1960). Maximum urine concentration is 400–500 mOsm/l; the

maximum plasma concentration is 400 mOsm/l (Greenbaum and Dicker, 1963). Reportedly, the kidney mitochondria are unaffected by vasopressin (Greenbaum and Dicker, 1963); however, vasopressin reduces urine flow, plasma osmolarity (to 295 mOsm/l), creatine excretion, and the urine : plasma ratio to 1:1.4 (Dicker and Eggleton, 1964). Variations in tubular water reabsorption cause urea and sodium concentrations to vary inversely in the urine (Schmidt-Nielsen and Pfeiffer, 1970). The "absence of looped vasa recta in *Aplodontia*" may prevent the efficient trapping of solute such as urea in the medullary interstitium" that may account in part for the poor urine-concentrating abilities (House et al., 1963:182). Because of the poor urine-concentrating abilities of the kidney, the concentration of excreted solutes in the urine was almost identical to that in plasma thereby requiring high intake of water by mountain beavers (Nungesser and Pfeiffer, 1965). This may account for the restriction in distribution of *Aplodontia* to the "wet west slopes of the . . . Pacific Northwest" (Nungesser and Pfeiffer, 1965:296).

Rectal temperature varied from 34.4°C after a 3-h period of inactivity, to 36–37°C during shorter periods of inactivity, to 37.5–38°C during normal activity, and to 38–38.5°C during extended forced activity (Fisler, 1965). The liver of mountain beavers is black, has an indistinct lobular pattern, and the hepatocytes have a granular pigmentation composed of melanin (Newton and Snyder, 1978).

The molars of *A. rufa* are characterized by flat and pitted lingual enamel crests on the occlusal surface that lacks detrital grooves (Rensberger, 1978). The lingual enamel has a convex anterior surface, and rods and interprismatic substances equally resistant to chemical abrasives. Most tooth wear in mountain beavers is caused by contact rather than food abrasion. The anterior edge of the teeth wears faster than the occlusal surface, but the lingual lamina of cementum prevents the formation of large flaked pits characteristic of teeth of other herbivorous rodents (Rensberger, 1978).

The cochlea of *Aplodontia rufa* has three and one-half turns, of which a narrow portion of the upper turn may be closed, and the scala tympani is constricted in the upper one and one-half turns (Merzenich et al., 1973). Mountain beavers have an unusually large dorsal cochlear nucleus characterized by only a small amount of laminar organization, heavily myelinated fibers in the central core, and a small dorsal stria. The even larger cochlear granule field is characterized by neurons 4–5 μm in diameter that have a "nucleolus that occupies about half of the volume of the nucleus" (Merzenich et al., 1973:335). These specializations are believed to allow mountain beavers to detect slow changes in air pressure within their burrows (Merzenich et al., 1973). The auditory ossicles are much like those found in Sciuridae except that the incus has a conical prominence between the articulating surfaces, the stapes has a translucent aperture in the base between the anterior and posterior crura, and the malleus lacks a orbicular apophysis but has lamina and cephalic processes (Cockerell, 1916).

The quadrangular-shaped scapula is formed by a large thin plate with a thick angulated vertebral border, a high spine for attachment of the rhomboid, anterior serratus, and levator scapulae muscles, and a large metacromion (Hill, 1937; Lewis, 1949). The long and curved clavicle has a prismatic shape in the middle and is compressed toward the ends (Lewis, 1949). The sternoclavicular joint permits circular motion because of its loose capsule. The humerus has multiple large, rough attachment surfaces and a trochlea with a deep sulcus and medial lip (Hill, 1937); the head of the humerus is nearly global and seems large for the roughly prismatic bone in proximal view. The ulna has a long and heavy olecranon that provides considerable mechanical advantage to the forearm extensors, a lateral keel extending from the olecranon to the styloid process, and is curved in two planes (Lewis, 1949). The radius has no pseudostyloid process (Hill, 1937). The femur has an incomplete trochanteric ridge and no third trochanter. "The sacral vertebrae are strongly fused and the lumbar transverse processes are reduced" (Fry, 1961:185).

In the head and neck region, mountain beavers lack some segments of the sphincter colli profundus muscle, there is a reduction in number of segments and size of the retroauricular muscle, cervicoauricular muscle, and muscles on the dorsum of the head, and a simplification of the nasolabialis, zygomaticolabialis, nasolabialis, profundus, and buccinatorius muscles (Klingener, 1970). Reduction of the cervicoauricular is associated with reduction in the size of the pinnae. The stylohyoideus muscle originates at the stylohyal cartilage instead of the jugular process as in pocket gophers (Geo-

myidae—Hill, 1937). The jugulohyoideus muscle, which does not occur in muroid or geomyid rodents, originates on the jugular process and inserts on the stylohyal cartilage. A few medial fibers of the genioglossus muscle insert on the hyoid apparatus. The wide hyoglossus muscle extends laterally from the hyoid to the tongue. The styloglossus originates from the stylohyal cartilage, instead of the jugular process as in geomyids, and inserts on the jugulohyoideus instead of the tongue (Hill, 1937).

In the region of the pectoral girdle, the large single-slip trapezius, unusually massive triceps, rhomboids, occipitoscapular, single deltoid, levator scapulae, and anterior serratus muscles attach to the immobile scapula (Lewis, 1949). The atlantoscapularis muscle inserts on the acromion. The triceps, and minimally the anconeus and dorsal epitrochlear muscles, allow for the powerful extension of the forearm. The flexor muscles of the pectoral girdle, the coracobrachialis, biceps, and brachialis, are greatly reduced in size. The supinator and pronator muscles are well developed; however, the structure of the proximal and distal radio-ulnar joints restricts movement to <90°. The pectoralis minor muscle inserts on the greater tuberosity of the humerus and is continuous with the xiphihumeralis muscle that originates on the xiphisternum and midventral aponeurosis (Hill, 1937). The elements of the wrist joint allow unlimited flexion and extension, but limited abduction and adduction (Lewis, 1949).

In the region of the pelvic girdle, the dorsal spinalis and semispinalis muscles, the caudofemoralis and presemimembranous, the gluteus longus and maximus, and the gluteus medius and piriformis are fused as pairs (Fry, 1961; Hill, 1937; Klingener, 1970). The tensor fasciae latae muscle is present, the gracilis is single, the adductor magnus has two segments, the gastrocnemius has three heads, and the internal obturator is large (Fry, 1961). The large internal obturator muscle originates from the entire surface of the pelvis (Hill, 1937). There are no supinator longus, sartorius, or brachioradialis muscles (Fry, 1961; Klingener, 1970; Lewis, 1949).

Aplodontia rufa retains the primitive rodent condition of the internal maxillary artery originating as one of the terminal branches of the external carotid artery (Guthrie, 1969). Mountain beavers lack stapedial and internal carotid arteries (Guthrie, 1969).

The brachial plexus has a primitive configuration and is formed from the spinal nerves of the fourth–eighth cervical segments and the first thoracic segment (Lewis, 1949). The lumbosacral plexus is formed from the "spinal nerves of the 4th, 5th, and 6th lumbar segments and the first through 5th sacral segments" (Fry, 1961: 181).

Mountain beavers have a prominent intermaxillary foramen, orbital foramina located dorsad of the alveoli of the upper cheek-teeth, a sphenopalatine foramen located dorsad of the posterior portion of P4, and an ethmoid foramen located dorsad of the M1–M2 interface and posterior of the sphenopalatine (Wahlert, 1974). No part of the masseter muscle passes through the fairly large infraorbital foramen (Hill, 1935). The small alisphenoid canal is located in the lateral pterygoid plate and contains the masticatory nerve and internal maxillary artery (Hill, 1935). The sphenopterygoid foramen is large and contains the internal maxillary vein. The two internal maxillary veins are connected by a vein that passes through the vascular canal located in the basisphenoid near the foramen ovale. There is no lacerum foramen for passage of a stapedial artery (Hill, 1935).

The interpeduncular nuclear complex in the brain of *A. rufa* has a subnuclear segment divided into distinct pars lateralis, pars medialis, pars dorsalis parvocellularis, and pars dorsalis magnocellularis sections (Ives, 1971). The pars dorsalis parvocellularis has the smallest cells and has a mean ($\pm \text{SE}$) area of $47.6 \pm 1.9 \mu\text{m}^2$. The pars dorsalis magnocellularis has the largest cells, cells that mingle with the cells of the nucleus centralis superior, and a mean area of $117.7 \pm 6.7 \mu\text{m}^2$. The pars lateralis and pars medialis have cells of the same size and a mean area of $82.5 \pm 3.2 \mu\text{m}^2$ and $72.6 \pm 3.1 \mu\text{m}^2$, respectively (Ives, 1971).

Aplodontia females have a typical duplex uterus, an elliptical ovary, a urogenital sinus proximal to the urethral opening, and a short mesosalpinx that connects the oviduct and ovary but does not form a bursa around the ovary (Pfeiffer, 1958). There are pectoral, thoracic, and abdominal pairs of mammary glands. The functional segments of the yolk sac are the bilaminar omphalopleure, that is extensive and persists until parturition, and the vascular splanchnopleure (Harvey, 1955). The germ disc has a mesometrial orientation and the blastocysts have a single implantation cone (Harvey, 1955). There is a well-developed choriovitelline placenta that persists until

the limb-bud stage, followed by a nonvascular, but functional, chorioptic placenta. Also, a discoid, nonlobate, hemochorionic chorioallantoic placenta is located in the mesometrium following the limb-bud stage (Harvey, 1955).

Aplodontia males have a penis ca. 45 mm long; paired elliptical, compound, and tubuloalveolar bulbourethral glands ca. 5 mm long; and seminal vesicles located within the ventral fascia of the prostate gland (Pfeiffer, 1956). The seminal vesicles are apparent only in breeding individuals when the vesicles are 1 cm long. Mature spermatozoa are ca. 100 μm long and "usually bear a large galea capitis when obtained from the vas deferens or epididymis" (Pfeiffer, 1956:633).

Seasonal variation in the pelage is slight; the wooly undercoat is always present and there is a single annual molt (Stangl and Grimes, 1987). Guard hairs are 17.5 by 0.084 mm in summer, 21.8 by 0.081 mm in winter, and circular in cross section. Pregnant and lactating females have patches of coarse black hairs around the nipples (Pfeiffer, 1955). In the areolar regions of the abdomen, the hair follicles are larger than follicles located elsewhere on the abdomen and the pigment in the dermis and epidermis, overlying the mammary gland tissue, is darker than surrounding tissue. Estrogen is involved in these hair and tissue changes when there is proliferation of the uterine glands (Pfeiffer, 1955).

ONTOGENY AND REPRODUCTION. Onset of reproductive activity in the mountain beaver is evidenced among males by rapid increase in size of the testes, and prostate and bulbourethral glands, and by the testes attaining a "semiscrotal" position (*A. rufa* has no true scrotum—Hubbard, 1922) in November or December (Hubbard, 1922; Lovejoy et al., 1978; Pfeiffer, 1956:632, fig. 2). Lovejoy et al. (1978:324) reported that in captivity both sexes commenced to produce "cloudy yellowish-milky urine" at this season when placed in a handling cage (Black and Hooven, 1973). At estrus, the female exhibits "hypertrophied nipples, a greatly swollen vulva, and a vaginal smear showing a cloud of cornified epithelial cells" (Pfeiffer, 1958:231). The preovulatory ovary may contain follicles as large as 3 mm in diameter (Pfeiffer, 1958). Yearling females ovulate (corpora lutea are formed) but do not breed (no spermatozoa found in reproductive tract); thus, ovulation is considered to be spontaneous (Pfeiffer, 1958).

Aplodontia rufa has a single annual estrous period with considerable intrapopulation synchrony among breeding females (Pfeiffer, 1958). Onset of estrus seemingly varies with locale as estimated dates of parturition ($n = 1-5/\text{locale}$) were as early as 6 February in Marin Co., California, and as late as 3 May in Jefferson Co., Washington (Pfeiffer, 1958). Date of parturition was not related strongly with latitude as it was 30 March for Placer Co., California; 22 March for Lane Co., Oregon; and 11 March–3 April for King Co., Washington (Pfeiffer, 1958). Duration of gestation was considered 28–30 days by Scheffer (1929) and Pfeiffer (1958) but 6–8 weeks by Hubbard (1922).

In *A. rufa*, litters of two and three are common, four less so (Dalquest, 1948; Lovejoy and Black, 1974; Lovejoy et al., 1978; Pfeiffer, 1956; Scheffer, 1929, 1930; Seton, 1929). Litter size, based on embryo counts, was reported as seven females with two embryos and nine with three (Scheffer, 1929). In Washington, mean litter size ($n = 12$) was 2.8 based on counts of corpora lutea and 2.4 based on counts of embryos (Pfeiffer, 1958). Based on counts of pigmented sites of implantation, 25 females had a mean of 2.5 young; three others, with an average of 2.7 corpora lutea, had an average of 2.7 pigmented sites of implantation (Pfeiffer, 1958).

Young are born either head first or in the breech presentation (Cramblet and Ridenhour, 1956). At birth, young are pink, naked, helpless, and blind, but able to emit squeaks and, within 20 min, to nurse (Cramblet and Ridenhour, 1956). Vibrissae are visible, but auditory canals and eyes are closed; the ear is formed but not extended; the front toes are well developed and clawed, the hind toes mere stubs; and the tail is noticeable (Cramblet and Ridenhour, 1956; Lovejoy et al., 1978). Sixteen hours after birth one of three young weighed 25.5 g and was 70 mm long; 25 h after birth the three young weighed 25.0, 26.5, and 29.5 g and were 85, 90, and 87 mm long, respectively (Cramblet and Ridenhour, 1956). These three individuals continued to grow in length, but gained little in mass after the 3rd day; all died on the 6th day after birth. Two other individuals weighed 18.0 and 21.6 g and averaged 66 mm long 2 days after birth; they did not squeak until 3 days old (Lovejoy et al., 1978); at 5 days, the skin was darkly pigmented on the

dorsum and pate; at 7 days, the skin was wrinkled, especially on the hind legs; at 9 days, a sparse pelage of fine hairs covered most of the body and the pinnae were free and erect; at 10 days, the eye slits were formed, but both eyes and ears remained closed; at 14 days, the pelage was complete with dorsal hairs dark and sleek, but ventral hairs were white; at 15 days, the young began to crawl solely by use of the front legs; at 21 days, the ears were open, and the hair was dark and more brownish; at 28 days, the lower incisors erupted; at 33 days, the upper incisors erupted and one individual was observed to scratch its face with a hind foot; at 35 days, the head was elevated and crawling by use of all four feet was observed; at 38 days, young began to eat solid food; at 45 days, one young had open eyes but the eyes of the other did not open until 9 days later (Lovejoy et al., 1978). Average mass for the two young was 27.9 g at 7 days and increased exponentially to 364.5 g at 60 days (Lovejoy et al., 1978:327, fig. 3).

The two captive young accepted natural foods in week 7, but continued to nurse in week 8; thereafter, both commenced to lose weight and both died in week 10 (Lovejoy et al., 1978). Maternal females lactate for ≤ 2 months (Pfeiffer, 1958).

In the wild, young mountain beavers probably are weaned by 6–8 weeks while still in the nest; thus, they likely feed on plants carried to the nest by the maternal female (Lovejoy and Black, 1974). In Benton Co., Oregon, the earliest capture of a young-of-the-year was on 3 June; it weighed 280 g, thus was considered to be about 7–8 weeks old (Lovejoy and Black, 1974). Mean rates of gain in mass among repeatedly live-trapped juveniles declined during June and July, plateaued in August, and remained so throughout the juvenile period (Lovejoy and Black, 1974). As yearlings, some individuals doubled their mass, attaining an average mass > 740 g within a year of becoming independent (Lovejoy and Black, 1974).

ECOLOGY. Within its range, *A. rufa* occurs in forested areas from near sea level to timberline (Camp, 1918; Dice, 1932; Sviha and Sviha, 1933). Most authorities agree that populations attain peak densities in areas in early to mid-seral stages vegetated by a tangle of second-growth tree species, shrubs, and forbs; containing debris remaining from earlier forests; and near water courses (Dice, 1932; Hooven, 1977; Scheffer, 1929; Sviha and Sviha, 1933). Mountain beavers are most abundant in high mountain parks in deciduous forests and least abundant in coniferous forests (Dice, 1932). The species also was reported as most numerous on slopes and foothills along the sides of gulches; a few occur in mature forests (Scheffer, 1929). Some authorities emphasized the role of running water as a habitat requirement, including water flowing through some sections of tunnels used by *A. rufa* (Lum, 1878; Seton, 1929), but others regard such situations simply as a hazard of occupying moist habitats near streams that support plants used for food (Johnson, 1971). Deep soils are a prerequisite for burrows constructed by mountain beavers (Camp, 1918). Although numerous, albeit somewhat disparate, descriptions of habitats used by the species are available; the habitat requirements for *A. rufa* do not seem to have been evaluated quantitatively.

Aplodontia rufa constructs extensive burrow systems (Camp, 1918); burrows are about 13–18 cm high by 15–25 cm wide (Hubbard, 1922) and radiate from nest sites (Martin, 1971). Systems are supplied with numerous openings (≥ 100 in a 0.46-ha area), but spoils of excavated earth are formed at only a few openings; unplugged burrow entrances usually are concealed by vegetation (Camp, 1918). Nearly all entrances are connected by tunnels constructed 15–46 cm below the surface; nest chambers about 30 cm in diameter contained dried leaves trampled into a flat pad (Camp, 1918). Nests were described as containing ≤ 35 l of vegetation and being 0.3–1.5 m below the surface (Martin, 1971). On one area in Washington, Johnson (1975) reported finding tentlike structures built of sticks, leaves, and succulent vegetation over entrances to mountain beaver burrows; he considered the tents to afford protection from rain entering the burrows. Outpockets in the walls of some of the larger tunnels contained roots, stems, and leaves, and were plugged with earth pellets (Camp, 1918). In California, *A. rufa* usually constructs burrow systems on north slopes, whereas in British Columbia they are constructed on south slopes (Camp, 1918). In Oregon, mean burrow temperatures did not vary $> 3^\circ\text{C}$ in any month and greatest daily variation was $< 4^\circ\text{C}$ (Johnson, 1971).

Relatively few studies of the population dynamics of *A. rufa* have been conducted; Camp (1918) removed 11 individuals from a 0.46-ha area and Voth (1968) removed 21 from a 2-ha area.

Estimated densities were 8.3 and 7.3/ha on 7- and 9-ha areas, respectively (Motobu, 1978). However, a population density as high as 15–20/ha was reported (Hooven, 1977); a description of the methods on which the estimate was based was not provided. Lovejoy and Black (1979a, 1979b) captured 181 individuals in 5,144 trap nights on a 5.5-ha area in western Oregon during a 20-month period; 10% of the mountain beavers they captured died in traps. The latter authors estimated densities of mountain beavers monthly by direct enumeration on a 10-ha area (5.5-ha trapping grid plus 40-m-wide boundary strip) at 4.1–5.4 animals/ha. By adding a 40-m boundary strip (mean distance between captures) to areas sampled by Camp (1918) and Voth (1968) estimates by these authors were nearly identical with the minimum estimate of Lovejoy and Black (1979b). Nevertheless, Lovejoy and Black (1979b) considered their estimates to be conservative and presented an estimate by the Lincoln Index for 1 month that caused them to suggest that the direct-enumeration method produced underestimates of the population they sampled.

The sex ratio of live-trapped juveniles ($n = 72$) was exactly 1:1, whereas that of adults ($n = 109$) was 1:1.6 in favor of males; the age ratio ($n = 181$) was 1:1.5 in favor of adults, including yearlings (Lovejoy and Black, 1979b). Lovejoy and Black (1979b: 88) considered the differential among sexes to be a "true ratio and not an artifact of trapping," but provided no evidence in support of their contention. Of 45 animals marked by Lovejoy and Black (1979b) during the first month of study, 29 (64%) were known to be alive 1 year later and 11 (24%) were known to be alive 2 years later. Some of these individuals were sexually mature when first captured, so were ≥ 4 years old when last captured. Based on these data, estimated longevity is 5–6 years (Lovejoy and Black, 1979b).

During collection of 75 *A. rufa* in Washington, Oregon, and California, in small leg-hold traps set in runways, nine *Spilogale gracilis*, four *Mustela frenata*, one *M. erminea*, one *M. vison*, eight *Neotoma fuscipes*, one *N. cinerea*, two *Tamiasciurus douglasii*, one *Zapus princeps*, four *Sylvilagus bachmani*, one *Microtus californicus*, one *M. richardsoni*, one *Thomomys bottae*, one *Peromyscus maniculatus*, and one *Dicamptodon ensatus* were captured (Pfeiffer, 1953). Other users of mountain beaver burrows include *Neurotrichus gibbsii*, *Scapanus orarius*, *Lepus americanus*, *Clethrionomys californicus*, *Phenacomys albipes* (Maser et al., 1981), *Mephitis mephitis* (Camp, 1918), *Procyon lotor* (Lord, 1866), *Taxidea taxus*, and *Martes pennanti* (Lum, 1878).

Remains of *A. rufa* occurred in only 12 (8.4%) of 143 fecal droppings of *Felis rufus* collected throughout the Coast Range of Oregon, constituting only 5.3% of the mass of prey eaten (Nussbaum and Maser, 1975). However, in the Cascade Mountains of Oregon, *A. rufa* occurred in 57 (14.1%) of 404 fecal droppings of *F. rufus* (Toweill and Anthony, 1988a) and in 70 (8.3%) of 844 fecal droppings of *Canis latrans* (Toweill and Anthony, 1988b). Where carnivore populations were not exploited in the Coast Range of Oregon, remains of mountain beavers occurred in 244 (79.0%) of 309 fecal droppings of *C. latrans*, and in 182 (73.7%) of 247 fecal droppings of *F. rufus* (Witmer and deCalesta, 1986). In Washington, 20–25% of the composition of feces of *C. latrans* was remains of *A. rufa* in May–July, but only 5% in August–September (Brigham, 1954). Mountain beavers occurred in one (1.6%) stomach and two (3.3%) colon tracts of *F. concolor* from the western Cascade Mountains of Oregon (Toweill and Maser, 1985). Skunks and weasels that use mountain beaver burrow systems may prey on nestlings and juveniles (Hooven, 1977). *Aquila chrysaetos* is known to prey on *A. rufa* (Servheen, 1978) and "owls are to be regarded as enemies" (Camp, 1918:533).

Ectoparasites recorded from *A. rufa* include Siphonaptera: fleas: *Epitedia jordani* (Hubbard, 1940a), *E. scapani*, *Ceratophyllus [Amonopsyllus] ciliatus protinus*, *Opisodasys keeni*, *Orlopsyllus [Diamanus] montana*, *Paratyphloceras oregonensis* (Lewis et al., 1988), *Dasypsyllus gallinulae perpinnatus*, *Dolichopsylla stylosus* (Hubbard, 1940b), *Hystrichopsylla schefferi* (includes *mammoti* and *hubbardi*—Lewis et al., 1988), and *Trichopsylloides oregonensis* (Hubbard, 1943); Acarina: mites: *Alphalaelaps [Laelaps] aplodontiae* (Jellison, 1945a; Radford, 1951; Whitaker et al., 1979), *Patrinynsus [Ichoronynsus] hubbardi*, *Haemogamassus reidi*, *Haemogamassus* sp. (apparently a new species), *Aplodontochirus borealis*, *Microlabidopus americanus*, *Aplodontopus latus*, *Euryparasitus* sp. (Whitaker et al., 1979), *Hirstilonynsus occidentalis* (Strandtmann and Morlan, 1953), *Neotrombicula aplodontiae* (Brennan, 1946; Wrenn and Maser, 1981), *N. cavigcola*, *Aplodontophila pacifica*, *Euschoengastia brennani*, and *Eus-*

choengastia sp. (Wrenn and Maser, 1981); and Coleoptera: *Lepitinillus aplodontiae* (Augustson, 1941; Jameson, 1949). *A. rufa* has the distinction of serving as the specific host for the enormous flea, *Hystrichopsylla schefferi* (males, 6 mm; females, 8 mm long), "conceded to be the largest flea known" (Hubbard, 1947:360), and a flea, *Trichopsylloides oregonensis*, that serves as a host to the phoretic nymphal instar (hypopus) of the acaridid mite *Trichopsylla oregonensis* (Fain and Baker, 1983).

Endoparasites include two Cestoda: *Taenia tenuicollis* (cysts of dead coenurei and cysticerci in 11 of 22 livers examined—Locke, 1955) and *Taenia pisiformis* (Hall, 1920). Doran (1954a, 1954b, 1955a, 1955b), in his exhaustive search of the literature on protozoan and helminth parasites of North America rodents, listed no endoparasites of the mountain beaver other than the latter cestode.

Plants used for food by *A. rufa* are extremely varied, but pteridophytes, especially sword fern, *Polystichum munitum*, and bracken fern, *Pteridium aquilinum*, constitute the greatest proportion of those eaten during most seasons (Hubbard, 1922; Voth, 1968). The latter fern and several other species eaten (Voth, 1968) or cached (O'Brien, 1981) by mountain beavers are toxic; Voth (1968) suggested that the mountain beaver specializes in foraging on plant species toxic to many other vertebrates. Most differences in diet by season, sex, or age may be related to protein requirements and availability; in October, the season in which the protein content of leaves of alder is highest, 77% of the diet of adult males in coastal Oregon is red alder, *Alnus rubra*. Adult females shift to a diet of conifers, then to the new growth of grasses and forbs in spring when lactating (Voth, 1968). The diet of juveniles resembles that of adult males except in June–August, when they consume more young grasses to obtain additional protein for growth (Voth, 1968). In the Sierra Nevada Mountains of California, conifers were foraged upon heavily by mountain beavers in autumn and winter at high elevations when their nutrient content was high and other plants were unavailable; in summer, conifers were avoided (O'Brien, 1988). Twenty-two percent of 900 trees and shrubs examined on a 138-ha area in western Oregon exhibited evidence of being clipped by mountain beavers (Crouch, 1968); *Acer circinatum*, *A. macrophyllum*, *Vaccinium parvifolium*, *Alnus rubra*, *Rhamnus purshiana*, and *Corylus cornuta* were clipped most frequently. Accounts are numerous of mountain beavers eating ferns (Anthony, 1916; Lum, 1878; Scheffer, 1929, 1952; Storer et al., 1944), *Gaultheria shallon* (Lum, 1878; Scheffer, 1929), *C. cornuta* (Lum, 1878), *Rubus parviflorus*, *Ribes*, *Mimulus* (Storer et al., 1944), *Acer*, *Prunus* (Scheffer, 1952), *Lysichiton americanum*, *Oplopanax horridum*, *Berberis aquifolium*, *Thuja plicata*, *Pseudotsuga menziesii*, *Tsuga heterophylla* (Scheffer, 1929), and numerous other species of plants (Camp, 1918; Voth, 1968).

Foraging by mountain beavers on seedlings in areas undergoing reforestation may cause extensive damage and economic loss (Black et al., 1969; Hooven, 1977; Neal and Borreco, 1981; Scheffer, 1929, 1952; Voth, 1968); occasionally, they cause damage to gardens (Scheffer, 1929) and forage crops (Lum, 1878). Damage to forests by mountain beavers was ranked fourth in frequency among five groups of small mammals in Oregon and Washington (Canutt, 1969). Of newly planted conifer seedlings, 12–20% were lost to mountain beavers in some areas (Hooven, 1977), but the level can be as high as 25% (Motobu, 1978). Damage to small trees as high as 3–4 m above the ground and girdling of large deciduous trees beneath the snow was attributed to mountain beavers (Couch, 1925; Scheffer, 1952). "Timing of canopy closure resulting in suppression of understory vegetation appears to have more influence on the occurrence of damage [by *A. rufa*] than tree size" (Neal and Borreco, 1981:84). Mountain beavers are considered to be "a major factor influencing woody-plant cover and composition" in Oregon (Crouch, 1968:152). Methods used to control depredations by mountain beavers are removing vegetation used for food and cover (mechanically, by use of herbicides, or by use of herbicides in combination with burning), population reduction by use of toxic baits and trapping, and by use of plastic-mesh tubes surrounding tree seedlings to prevent clipping (Hooven, 1977). Number 0 and number 1 steel traps were used to trap *Aplodontia* (Fry, 1961). More than 50% of mountain beavers resident on a 7-ha area were killed by fire after vegetation was treated with a herbicide, but only 19.7% were killed on a 9-ha area treated similarly but that contained a 1.8-ha area that did not burn; most survivors on the 9-ha area were captured in the unburned portion (Motobu, 1978).

Numerous authorities noted small piles of wilted and partly

dried vegetation nearby or in the entrances to mountain beaver dens and stated or implied that the material was hay being cured by mountain beavers (Hooven, 1977; Lum, 1878; Merriam, 1896; Seton, 1929). Such activity commences in August (Hamilton, 1939). Most authorities indicate that the material is moved into the burrow and eaten, whereas Camp (1918) and Scheffer (1929) claimed that it is not eaten but used as nesting material. Both functions are likely; the wilted material may be eaten and the dry material used in the nest (Maser et al., 1981). Hooven (1977) indicated that body mass of mountain beavers that survived an application of herbicide followed by a controlled burn to remove vegetation did not decline, indicating that they were feeding on stored materials. Voth (1968) hypothesized that mountain beavers harvested dried vegetation for nesting material, but cut, partly cured, and ate the partially cured material to adjust their water intake. An alternative hypothesis was that the cutting and piling of vegetation was related to the security of mountain beaver food supplies during periods when foraging was unsafe (Voth, 1968). In northeastern California, food caches accumulated by two or more mountain beavers were 58.3% *Delphinium glaucum*, 20.7% *Alnus tenuifolia*, 18.2% *Corydalis caseana*, 1.5% *Verastrum californicum*, and 1% other species (O'Brien, 1981). Obviously, mountain beavers were selective of plants stored as *D. glaucum* and *A. tenuifolia* composed only 8 and 5% of the vegetative cover, respectively, but unnamed species in caches composed 30% of the vegetative cover (O'Brien, 1981).

As a marking technique, 15–35 mg/kg rhodamine B administered as a single dose by oral gavage produced bands that fluoresced orange under ultraviolet light 1–4 mm long in nails within 2–4 days and 1–2 mm long in vibrissae and guard hairs within 5–7 days. Free-living mountain beavers were marked similarly by ingesting apple baits containing ≥ 13 mg/kg of the dye. Marks lasted 19–26 weeks in hair and 13–21 weeks in claws of caged animals and 17–28 weeks in hair but only 6 weeks in claws of free-living animals (Lindsey, 1983). A 50% dextrose solution administered by oral or rectal gavage reduced mortality in mountain beavers resulting from shock of trapping and handling; no quantitative data on rate of success was provided (Dodge and Campbell, 1965). Radio transmitters mounted in "break-open collars which closely encircle the animal's neck" were used successfully (Dodge and Church, 1965: 118).

BEHAVIOR. The mountain beaver is largely fossorial; it rarely ventures more than a few meters from its burrow entrance. Despite statements to the contrary (Grinnell and Storer, 1924; Scheffer, 1929), *A. rufa* can climb trees (Ingles, 1960; Seton, 1929). It uses the stumps of previously cut branches much in the manner of rungs in a ladder to ascend or descend headfirst. It sometimes forages by pruning twigs from trees ≤ 6 m above the ground (Ingles, 1960). *A. rufa* also enters the water and swims well (Anthony, 1916; Ingles, 1954).

More commonly, to exploit a suitable clump of vegetation, *A. rufa* digs a new tunnel to the vicinity and makes short sallies to cut stems or fronds which it transports to its burrow where it feeds (Camp, 1918). While eating, *A. rufa* grasps food with the partly opposable pollex on the forepaws as it sits on the tail with hind feet positioned ventrally and soles facing forward (Camp, 1918). While defecating, *A. rufa* squats with tail and partially everted anus positioned upward; hard pellets are taken into the mouth and, "with an upward jerk of the head," tossed into a latrine (Kindschy and Larrison, 1961:2), whereas soft pellets are reingested (Ingles, 1961). Soft pellets are approximately four times the volume of hard pellets. In the large intestine, soft pellets are intermixed with hard pellets, and stomachs of some mountain beavers taken in the wild possess unmistakable remains of reingested soft pellets (Ingles, 1961).

Although most burrowing activity occurs in summer and above-ground activity nearly ceases in winter, mountain beavers do not hibernate (Ingles, 1959). In summer, they have five–six bouts of foraging each 24-h period. Nevertheless, they are 50–60% more active at night than during daylight hours (Ingles, 1959), prompting reports of their chiefly nocturnal activity (Grinnell and Storer, 1924; Scheffer, 1929). Lawrence and Sherman (1963) described a device to record activity in mountain beaver burrows, but it was not able to discriminate among species using the burrows.

Home-range areas calculated as range length times range width for individuals captured seven or more times at five or more trap sites averaged ($\pm SE$) 0.32 ± 0.05 (range, 0.09–0.70; $n = 14$) ha for adult males and 0.17 ± 0.05 (range, 0.05–0.40; $n = 7$) ha for

adult females. Similar data for juveniles were 0.13 ± 0.3 (range, 0.04–0.24; $n = 7$) ha (Lovejoy and Black, 1979a). Home-range areas calculated by the minimum-area method for 10 adults of both sexes radiotracked for 3–19 months averaged 0.12 (range, 0.03–0.20) ha (Martin, 1971); both maximum and minimum calculated areas were for individuals monitored for >12 months. Maximum movements from the nest for these individuals were 42.6 and 36.6 m, respectively. Two of 11 subadults made extensive linear movements considered by Martin (1971) to be dispersal: a female moved 564 m; a male moved 188 m, stayed 8 days at the site, then moved an additional 191 m and remained 46 days until contact was lost (Martin, 1971).

The mountain beaver is not a social animal although in some habitats animals may be crowded together such that their tunnels "fairly . . . honeycomb the ground" (Scheffer, 1929:4). Individuals fight when placed together in captivity, even in 0.1-ha enclosures (Godin, 1964). Although home ranges may overlap, nests and burrows are defended, with individuals exhibiting considerable fidelity to the nest site (Martin, 1971). However, Lovejoy and Black (1979a: 400) indicated that individuals "frequented one or two nest sites." In captivity, mountain beavers reportedly become docile quickly (Davis, 1941).

The mountain beaver has limited ability to see and hear, but tactile and olfactory senses are well developed (Camp, 1918; Scheffer, 1929). Seton (1929) suggested that the strong musky odor of the mountain beaver might be associated with intraspecific communication. The vocal repertoire of *A. rufa* is controversial; early naturalists attributed whistles and booming sounds to the mountain beaver (hence, the vernacular name "boomer"), but Scheffer (1929) attributed these sounds to birds and other mammals. Apparently, the only sounds produced by *A. rufa* are a soft whining and sobbing sound when in pain (Kindschy and Larrison, 1961), a grating sound produced with the teeth (Camp, 1918), and a high-pitched squeal when fighting (Godin, 1964) or when apparently frustrated (Kindschy and Larrison, 1961).

GENETICS. In both *A. r. californica* and *A. r. phaea*, $2n = 46$ with six pairs of metacentric and 16 pairs of submetacentric autosomes; the Y-chromosome is submetacentric (McMillin and Sutton, 1972). In *A. r. pacifica* there are five pairs of metacentric and 17 pairs of submetacentric autosomes; the Y-chromosome is metacentric (Carrasco and Humphrey, 1968). The karyotype is considered to be advanced because it contained no acrocentric autosomes (McMillin and Sutton, 1972).

Hemoglobins of *A. rufa* migrate anodally (Johnson and Wicks, 1959). A piebald condition on the underparts and sides is common (Anderson and Russell, 1957; Couch, 1926; Maser et al., 1981). Albino (Jewett, 1935) and melanistic (Fisler, 1965; T. E. Lawlor, in litt.) individuals occur.

REMARKS. The generic name *Aplodontia* was derived from the Greek *haploos* meaning single or simple, and *ondontos* meaning tooth. The specific name *rufa* was derived from the Latin *rufus* meaning reddish (Jaeger, 1978).

Aplodontia rufa has been referred to by a wide variety of vernacular names including mountain boomer, gehalis, farmer, ground bear, giant mole, sewel, showhurl, showl, shote, swak-la, o-gwäl-lal, ou-ka-la, ne-ta-te, and waw-kaw-see (Taylor, 1918). From 1817 to 1904, 30 variations on the spelling of *Aplodontia* were applied in publications (Coues and Allen, 1877; Taylor, 1918) ranging from *Haplodon*, *Hapludon*, *Haploodon*, *Haplodus*, and *Haploudontia*, to *Apluodonta*, *Aplodontie*, *Aplodontia*, and *Aplodontia*.

Because of its primitive nature and unusual characteristics, *Aplodontia rufa* variously was referred to the family Prensiculantia (which included *Castor*, *Mus*, and *Tamias* among others); section Sciurina of the family Muridae, order Glires; family Cunicularia (which included arvicolines and geomysids among others); the Pseudostomidae (pocket gophers); subfamily Castorinae; the porcupines (presumably Erethizontidae); and family Sciuridae from 1829 to 1877 (Taylor, 1918). However, according to Coues and Allen (1877), Lilljeborg (1866) raised *Haplodon* to familial rank (Haplodontidae), thereby removing it from the subfamily Castorinae of the family Sciuridae; he considered it nearest porcupines in taxonomic affinity. Subsequently, Gill (1872) separated *Haplodon* from other Glires rodents by raising its rank to that of superfamily (Haplodontioidea).

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